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Rooting patterns of *Rumex* species under drained conditions

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Root development and architecture were studied in three *Rumex* species growing in a perforated soil system in the greenhouse. Distinct differences in vertical root distribution under drained conditions were found among the three species. *Rumex acetosa* and *R. palustris* had a relatively superficial root pattern, whereas in *R. crispus* much of the root growth was concentrated in lower soil layers. In the upper soil layer the relative growth rate of the roots of *R. palustris* was significantly larger than that of the other species. A relation between the characteristic rooting patterns under drained conditions and the *Rumex* zonation in the field is discussed.

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Le développement et l'architecture racinaire ont été étudiés chez trois espèces du genre *Rumex*, poussant en serre dans un système de sol perforé. Des différences marquées dans la distribution verticale des racines sous des conditions d'assèchement ont été trouvées entre les trois espèces. Le *R. acetosa* et le *R. palustris* avaient des racines relativement superficielles tandis que chez le *R. crispus*, une bonne partie du système racinaire se retrouvait dans les couches profondes du sol. Dans la couche supérieure du sol, le taux relatif de croissance des racines du *R. palustris* était de loin supérieur à celui d'autres espèces. Les auteurs discutent d'une relation entre les caractéristiques des modèles d'enracinement sous des conditions d'assèchement et le zonage de *Rumex* aux champs.

[Traduit par la revue]

Introduction

This study is part of a project investigating the effects of irregular flooding, which may occur even during the growing season (Steeg 1984; Brock *et al.* 1987), on the distribution, the population biology, and the physiological processes in three *Rumex* species occurring in a river area (Blom 1985). These species are distributed along a flooding gradient. *Rumex acetosa* is found on high, seldom-flooded dykes and river levees. *Rumex palustris* occurs in very low, frequently inundated banks of former riverbeds. *Rumex crispus* has an intermediate position on the gradient (Fig. 1).

Since the first effects of waterlogging occur in the soil, special attention is given to the root systems of the species under study. A direct effect of inundation is a major decrease in gas exchange between the atmosphere and the soil (Armstrong 1979; Ponnamperna 1984). Any oxygen remaining in the soil is soon exhausted as a result of root and soil micro-organism respiration (Ponnamperna 1984). Waterlogged roots must therefore function in almost anaerobic soils. A known phenotypic response to waterlogging is an altered vertical distribution of roots; they tend to be concentrated in the upper soil layers (Etherington 1983; Jackson and Drew 1984). Such a response is also known in flood-tolerant *Rumex* species, e.g., *R. palustris* (L. A. C. J. Voeselek, C. W. P. M. Blom, and R. H. W. Pouwels, to be published). An altered distribution is probably related to the better aerated upper soil layer under waterlogged conditions (Jackson 1985).

In a series of papers (to be published) the effects of changing water levels on the rooting patterns, biomass production, flowering capacity, and seed production will be discussed. This paper focusses on the rooting patterns of *R. acetosa*, *R. crispus*, and *R. palustris* under drained conditions. Drained conditions occur in the river area between subsequent floodings. A recently developed nondestructive root observation method was used to study the root development and architecture under well-drained conditions.

Materials and methods

Plant species and field observations

In the Netherlands *Rumex acetosa* L. and *R. crispus* L. are common species of grasslands; *R. palustris* Sm., however, occurs most frequently on mud flats. Both *R. acetosa* and *R. crispus* are perennial species (Salisbury 1961; Hume and Cavers 1982), and *R. palustris* is biennial. *Rumex acetosa* has a fibrous root pattern, whereas the root systems of both *R. crispus* and *R. palustris* are dominated by a taproot (Kutcher 1960). The seeds of *R. acetosa*, *R. crispus*, and *R. palustris* were collected in 1985 at locations near the Waal, a major river of the Rhine delta. All seeds were stored in the dark at room temperature until they were used for this experiment. To obtain an impression of the occurrence of the *Rumex* species in relation to the environmental factors under study, the duration of floodings in *Rumex* zones in the growing season were recorded from 1980 to 1986. The pore volumes of 100-cm³ soil samples collected in the field from 2–6 and 10–14 cm below the soil surface were determined with a vacuum air pycnometer (cf. Noë and Blom 1981).

Methods

Roots were studied by means of a nondestructive observation method, the so-called horizontally perforated soil system (Tweel and Schalk 1981; Bosch 1984). In this system 99 perforations (each with a diameter of 12 mm) are bored through a soil monolith (height, 420 mm; width, 270 mm; depth, 185 mm) before seeds are planted. The distance between the perforations was 15 mm. The root segments and root apices in the perforations were observed with the aid of an intrascope (see Fig. 2). According to Bosch (1984), the natural development of roots is not influenced by the perforations, provided the diameter is not larger than 15 mm. Counting of all root segments and root apices in the perforations allows the estimation of both root length and number of root apices present in the total soil monolith. However, the root systems studied must satisfy two conditions: (i) distribution of root density is the same in and outside the perforations and (ii) density of all roots is equal in all directions. Root length and the number of root apices can be calculated according to the following equations (Bosch 1984):

$$[1] L_T = n_r(\pi wh/2md)$$

$$[2] M_t = n_r(wh/m0.25\pi d^2)$$

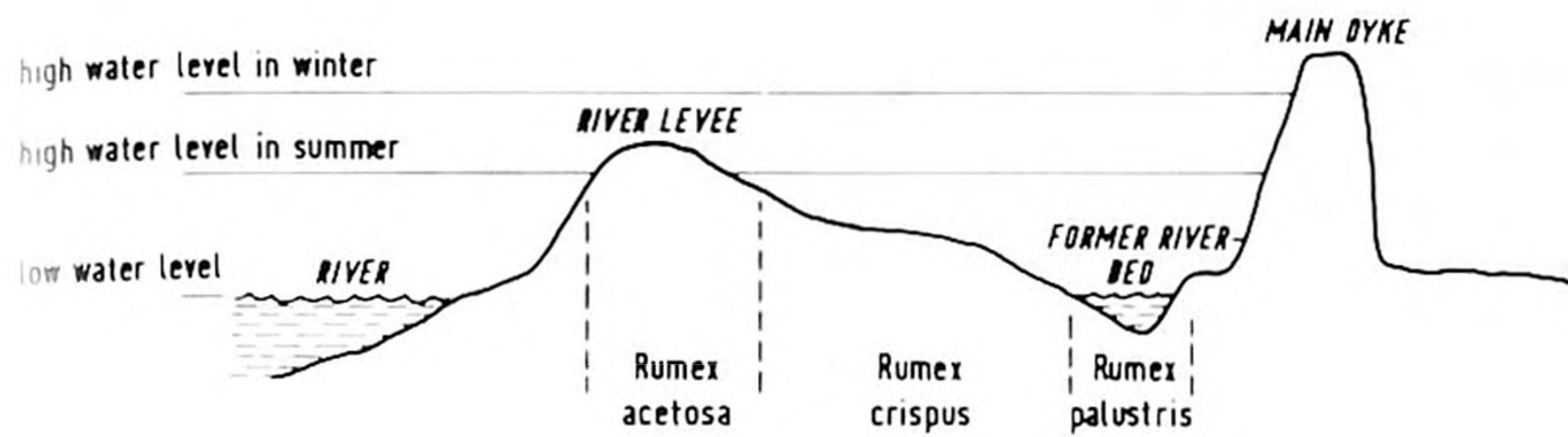


FIG. 1. The zonation of *R. acetosa*, *R. crispus*, and *R. palustris* in the river foreland of the Rhine.

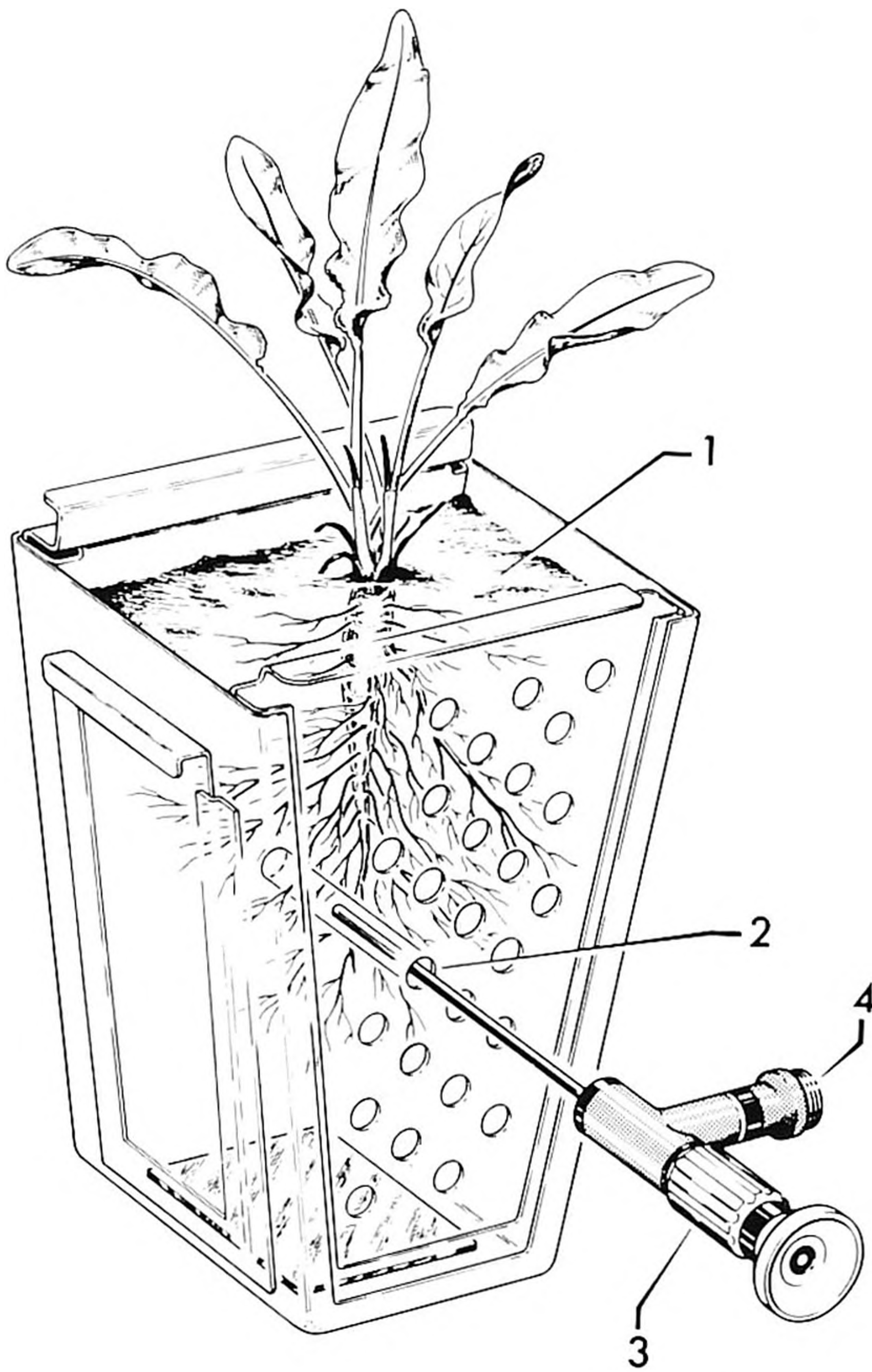


FIG. 2. The perforated soil system: 1, soil; 2, perforation; 3, intrascope; 4, connection for light source.

where L_T is the approximate total root length (m); n_r is the number of observed root segments (root apices are counted as half a root); w is the width of front plate (m); h is the height of soil monolith (m); m is the number of sampled perforations; d is the diameter of the perforations; M_i is the estimated number of root apices; and n_i is the number of observed root apices.

To provide an indication of the vertical distribution of the roots, the soil monolith was divided into six soil segments, each with a height of 70 mm. In each segment the total root length and the number of root apices were calculated. At the end of the experiment the total root length in the soil monolith was also measured with the line intersect method (Head 1966; Newman 1966; Rowse and Phillips 1974), using a Comair root length scanner (Comair, Melbourne). In this paper, root development (increase in root length) is presented as relative growth rate (RGR) analogue to the relative growth rate first described by Fisher (1921).

Experimental design

The experiment was carried out during the winter of 1986. The seeds were planted just below the soil surface, in 12 soil monoliths

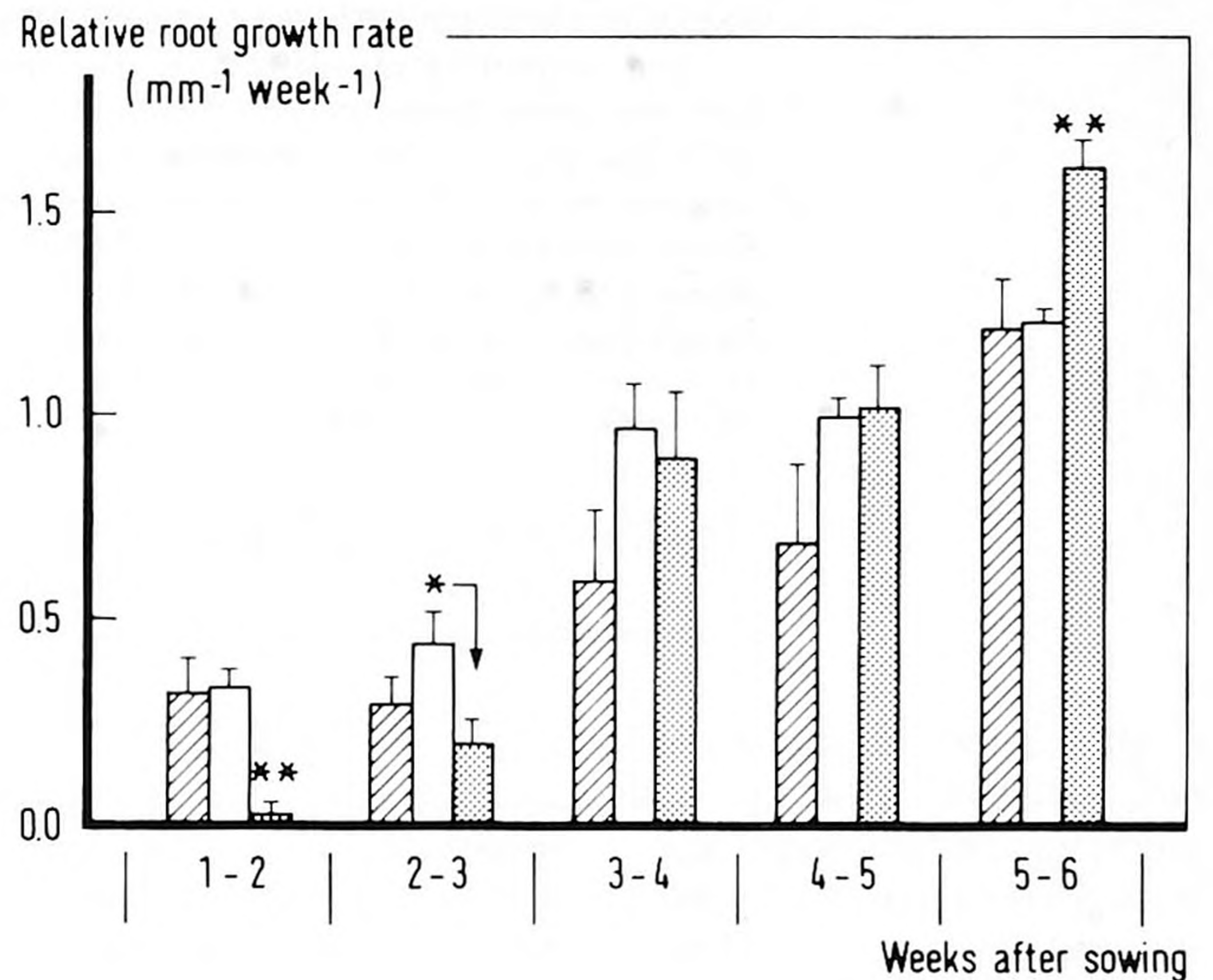


FIG. 3. The mean relative growth rate of roots of *R. acetosa* (▨), *R. crispus* (□), and *R. palustris* (▤) per period of 1 week (± 1 SE). **, significantly different from both other species ($P < 0.05$); *, significantly different from one other species ($P < 0.05$).

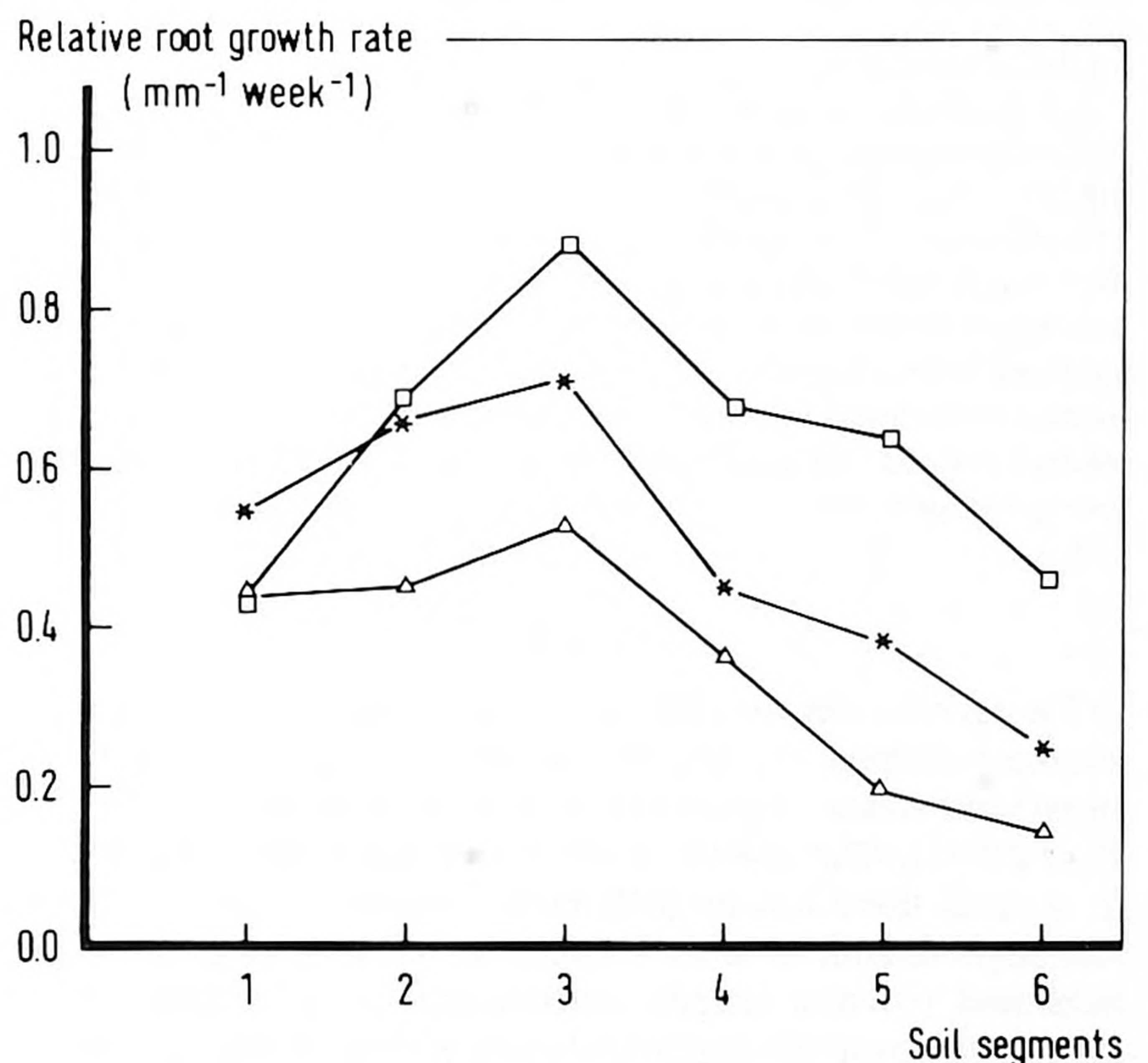


FIG. 4. The mean relative growth rate of roots of *R. acetosa* (△), *R. crispus* (□), and *R. palustris* (*) per soil segment (each soil segment has a height of 70 mm; soil segment 1 is located near the surface of the soil monolith, whereas layer 6 reaches the bottom).

(four per species), in a substrate of sand and potting compost (3:1, v/v). Five seeds were planted in each soil monolith. This number was reduced to one just after seedling emergence (approximately 1 week after sowing). The soil monoliths were watered carefully every day, and once a week Hoagland's nutrient solution diluted to 25% was used. During the experimental period the temperature in the greenhouse varied from 15°C at night to 20–24°C during the day (photoperiod 16h). At regular intervals after sowing (2, 3, 4, 5, and 6 weeks) the root segments and root apices in the perforations were counted. The root system of most plants reached the bottom of the soil monolith after 6 weeks of growth. Therefore, immediately after the

TABLE 1. The mean root length in metres (± 1 SE) measured with the line intersect method and the perforated soil system. The results of the paired *t*-test are also presented

Species	Perforated soil system	Line intersect method	<i>t</i> *	<i>P</i>
<i>Rumex acetosa</i> (n=4)	23.0 \pm 4.0	19.7 \pm 3.0	1.15	0.33
<i>Rumex crispus</i> (n=4)	54.3 \pm 1.9	43.4 \pm 3.7	2.86	0.06
<i>Rumex palustris</i> (n=4)	43.8 \pm 4.0	33.4 \pm 2.5	3.61	0.04

**t*, sample statistic of *t*-distribution.

TABLE 2. Number of root apices per metre root length of the whole root system during several weeks after sowing

	Weeks after sowing				
	2	3	4	5	6
RA	76.68(34.32)	46.57(23.30)	34.28(8.54)	16.87(3.66)	15.72 (2.15)
RC	28.69(14.32)	32.18(15.78)	26.62(7.42)	21.98(1.91)	22.96*(1.86)
RP	34.04(34.04)	28.36(17.02)	23.83(3.15)	17.36(2.89)	16.45 (1.07)

NOTE: RA, *R. acetosa*; RC, *R. crispus*; RP, *R. palustris*. Values in parentheses are standard errors.*Significantly different from both other species (*P* < 0.05).

root counts in week 6 the plants were destructively harvested to measure the root length with the Comair root length scanner. The fresh and dry weights of the roots were determined.

Statistical analyses

All statistical analyses were performed by means of the SAS statistical package. A paired *t*-test was used to analyze the data from the two sets of root length measurements (after log transformation). The influence of the species on the number of root apices per metre root length (after arcsin transformation), the root weight per metre root length (after arcsin transformation), and the RGR of roots were analyzed with a one-way ANOVA. Comparisons of means were performed with Fisher's contrast test. The influence of the species on the relative vertical root length and root apex distribution was tested with a nonparametric test, i.e., the Kruskal-Wallis test (Sokal and Rohlf 1981).

Results

The relation between the root length measured with the line intersect method (*y*) and the perforated soil system (*x*) was significant (linear regression: $y = 3.69 + 0.70x$; $R^2 = 0.82$; $P < 0.001$). The results of the paired *t*-test show that within *R. acetosa* there was no difference between the two methods. Although considerable differences between calculated (*x*) and measured (*y*) root lengths were found in *R. crispus*, these differences were not statistically significant. Within *R. palustris*, however, there was a significant difference between both root length methods (Table 1).

A summary of the mean RGR of roots of the *Rumex* species for each weekly period is given in Fig. 3. The results of the ANOVA are included in this figure. The RGR of the roots of *R. palustris* was relatively small during the first 2 weeks. After this period an increase in RGR took place, leading to the highest rate for this species in weeks 5 to 6.

The mean RGR of root systems of *R. acetosa*, *R. crispus*, and *R. palustris* per soil segment are presented in Fig. 4. The highest RGR for all species was reached in soil segment 3. Furthermore, it can be seen from Fig. 4 that *R. palustris* had a relatively high RGR in soil segment 1, whereas the other two *Rumex* species had lower RGR values ($P = 0.06$ in both comparisons).

Figure 5 gives the relative vertical distribution of the root

TABLE 3. Floodings in *Rumex* zones in the growing seasons (April–October) in 1980–1986

Plant zone	Year	No. of floodings	Duration (days) of longest flooding period
<i>Rumex acetosa</i>	1980	1	14
	1981	1	5
	1982	0	—
	1983	2	10
	1984	0	—
	1985	0	—
	1986	0	—
<i>Rumex crispus</i>	1980	2	38
	1981	4	18
	1982	2	8
	1983	2	82
	1984	4	21
	1985	3	11
	1986	3	39
<i>Rumex palustris</i>	1980	5	85
	1981	6	50
	1982	6	25
	1983	1	106
	1984	6	51
	1985	4	108
	1986	3	98

length and the relative number of root apices after 6 weeks of growth of the three *Rumex* species at different depths in the soil. It is clear that *R. acetosa* and *R. palustris* had the greatest root length and the largest number of root apices in the uppermost soil segment. For *R. crispus* the situation was different, i.e., the greatest root length and the largest number of root apices were located in the second segment.

Table 2 presents the number of root apices per metre root length. The results of the ANOVA indicate that *R. crispus* has significantly ($P < 0.05$) more root apices per metre root length than either of the other *Rumex* species after 6 weeks of growth.

The mean dry weights per metre of root after the destructive harvest were 4.07 ± 0.19 , 5.22 ± 0.39 , and $3.81 \text{ mg} \cdot \text{m}^{-1} \pm$

TABLE 4. Mean pore volumes at two depths in the soil in three *Rumex* zones in the river foreland of the Rhine

Zone	Depth (cm)	Total pore volume (%)	Water-filled pore volume (%)	Air-filled pore volume (%)
<i>Rumex acetosa</i>	2–6	56.0(6.2)	19.0(2.0)	35.5(7.0)
	10–14	50.3(1.3)	19.8(1.0)	30.5(1.9)
<i>Rumex crispus</i>	2–6	67.3(1.5)	31.0(4.6)	38.3(4.1)
	10–14	51.0(7.9)	28.0(7.5)	23.0(3.2)
<i>Rumex palustris</i>	2–6	65.3(6.9)	50.8(6.3)	14.5(3.0)
	10–14	62.0(6.8)	56.8(6.8)	5.3(2.8)

NOTE: Samples were taken within 1 week between two floodings. Values in parentheses are standard deviations.

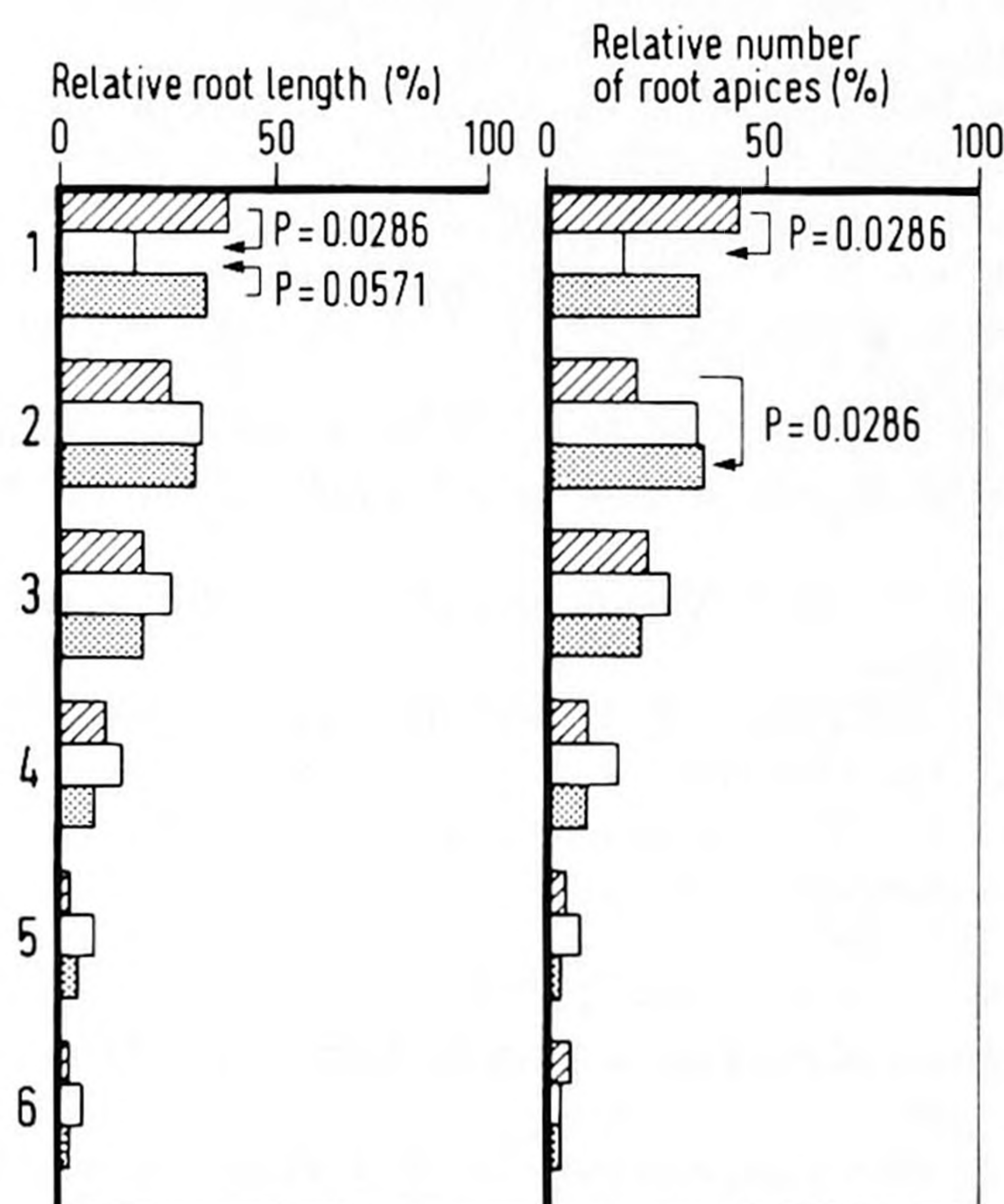


FIG. 5. The relative vertical distribution of the root length and the number of root apices 6 weeks after sowing (▨, *R. acetosa*; □, *R. crispus*; ▤, *R. palustris*). The results of the Kruskal–Wallis test are included.

0.50 SE for *R. acetosa*, *R. crispus*, and *R. palustris*, respectively. The results of the ANOVA indicate that the roots of *R. palustris* are lighter per unit length than those of *R. crispus*, whereas no significant differences were found for root weight of *R. acetosa* in comparison with those of the other two species.

Discussion

This paper emphasizes the importance of root length and the number of root apices in quantifying the root system. Root length and number of root apices are better gauges of the capacity for roots to absorb water and nutrients than root weight (e.g., Gardner 1964; Böhm 1976). The number of root apices gives a good indication of the branching intensity. From the comparisons of the root lengths measured with the perforated soil systems and the line intersect method (Table 1) it appeared that *R. acetosa* fits best in the model described for the perforated soil system. The root lengths calculated for both *R. crispus* and *R. palustris* more or less deviate from the real values (line intersect method). We presume that this might have been caused by the root patterns of *R. crispus* and *R. palustris* not fitting the conditions stated for equation 1, that the density of roots must be equal in all root directions. The root systems of *R. crispus* and *R. palustris*, both dominated by

a taproot, have a relatively oblong nature, with only a restricted number of horizontally growing laterals. The formula by which the root length was calculated will therefore overestimate the number of horizontally growing laterals. As a consequence the calculated root length will be overestimated. In conclusion, it can be stated that the precision of estimation of root length and number of root apices depends on the specific root architecture of that species.

During the first weeks of the experiment *R. palustris* showed a low RGR of roots, which is probably related to the low seed weight ($0.46 \text{ mg} \pm 0.08 \text{ SD}$; length, $1.66 \text{ mm} \pm 0.11 \text{ SD}$; width, $0.98 \text{ mm} \pm 0.07 \text{ SD}$) and therefore to the restricted endosperm reserves. The seeds of *R. acetosa* and *R. crispus* had mean weights of respectively $0.98 \text{ mg} \pm 0.25 \text{ SD}$ (length, $2.00 \text{ mm} \pm 0.21 \text{ SD}$; width, $1.23 \text{ mm} \pm 0.14 \text{ SD}$) and $1.72 \text{ mg} \pm 0.36 \text{ SD}$ (length, $2.10 \text{ mm} \pm 0.20 \text{ SD}$; width, $1.42 \text{ mm} \pm 0.16 \text{ SD}$), respectively. A relation between low seed weight and a smaller root growth is also described by Asher and Ozanne (1966), Evans (1970), and Stebbins (1971).

Rumex palustris showed in weeks 5 to 6 a higher RGR of the roots than each of the other *Rumex* species (Fig. 3). Compared with *R. acetosa* and *R. crispus*, the roots of *R. palustris* grew faster in the upper soil segment (Fig. 4). Similar to *R. palustris*, *R. acetosa* concentrates a relatively large part of the total root length in the upper soil layer (Fig. 5). However, this species is characterized by lower RGR values. At the end of the experiment the root systems of both *R. acetosa* and *R. palustris* are characterized by relatively long and less branching roots, whereas the root system of *R. crispus* consists of relatively short, frequently branching roots (Table 2).

The study proved that root development and architecture of both taproot species differ distinctly. It is possible that these differences are related to the positions of both species in the field. *Rumex palustris* is found in the river area on very low mud flats, where flooding occurs frequently and during long-standing periods (see Table 3). A relatively superficial root pattern can be an important advantage in such an environment. Between two periods of flooding the uppermost layer is the only part of the soil that is aerated to some extent. The deeper soil layer has a very low air-filled pore volume (Table 4). During and after floodings the shallow nature of the root system enables plants to exploit the relatively oxygen-rich upper soil layer. *Rumex crispus* is mainly found on higher parts of the river area, which are also frequently flooded. However, the duration of most floodings is very short (see Table 3). The air-filled pore volumes are much higher in this zone (Table 4). *Rumex acetosa* occurs on high dykes or river levees where flooding is nearly absent (see Table 3). Factors such as competition, drought, and soil compaction determine the root pattern

of this species. The results of our experiment strongly suggest that differences in rooting patterns among the species can be related to the natural occurrence of the three *Rumex* species in the field.

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